第34卷 第1期
1996年1月

古脊椎动物学报
VERTEBRATA PALASIATICA

pp. 27—40
figs. 1—3

山西榆社上新世犬类一新属

理·戴福德
(美国自然历史博物馆 纽约 10024)

邱占祥
(中国科学院古脊椎动物与古人类研究所 北京 100044)

摘要 新建属 *Eucyon* 是广布于古北区的一类犬科动物，在特征上介于狐和犬族之间。它具有狐类所没有的额窦，但其下裂齿的跟座上却没有犬族所特有的横嵴. *E. davisi* 是属型种。它最早发现于北美中中新世晚期，现在榆社上新世地层中也已发现. *E. zhoui* 比属型种个体稍大，为亚洲土著种。

关键词 山西 榆社，上新世，犬科

本文前一作者和泰勒 (B. E. Tayler) 正在总结北美的犬科化石 (在出版中)。在该文中他们已经指出，梅理阿 (J. C. Merriam) 1911 年根据俄勒冈早海费里 (Hemphillian) 地层中很少的一点材料所定的一个种，"*Canis*" *davisi*，是美国晚中新世时化石非常丰富的一个种。分支系统学的分析表明，这个种乃是南美一些属和进步的真犬的共同祖先。贝塔 (A. Berta，1988) 在她对南美大型犬类的分析中就已经发表了这一观点。现在看来，这一祖先类型在整个欧亚大陆的一些上新世地点中都有，而且有几个种。在榆社县云簇和泥河两个次盆地的高庄和麻则沟组中，就有这个属的保存很好的头骨和下颌。为了当前研究工作的需要，我们不得不在北美犬科化石专著出版之前先行发表对这一祖先类型的简单记述，这样才能把这些信息尽快地告知那些正在研究这类化石的同行们。

我们知道，这个新建的属会是复系的，因为它位于犬族这一分支的相当原始的基部。在这个新属的已知种中，没有任何一个具有更进步的性状。只有 *Eucyon zhoui* 具有一些真犬的特征。如果对它了解得更多一些， 也许可以把它归到真犬这一支的原始成员中。

科 Canidae Gray，1821

亚科 Caninae (Gray)，1821

族 Canini (Gray)，1821

***Eucyon* n. gen.**

属型种 *E. davisi* (Merriam)，1911。

特征 与狐族，包括化石的 (*Leptocyon*) 和现生的 (*Vulpes*，*Urocyon* 和 *Otocyon*)

收稿日期：1995-01-10

狐类在内，区别是它具有下列三个与犬族（南美犬类，*Canis*，*Cuon* 和 *Lycaon*）相同的近裔性状：具额窦，此窦侵入眶后突，使此突顶面上的所谓的“狐凹”消失；副枕突向后伸，末端通常很突出；乳突扩大成圆丘形或嵴形突起。但是这个属没有所有其它犬族成员所共有的一个特征，即下裂齿跟座上连接下次尖和下内尖的横嵴。另一方面，*Eucyon* 的第四下前臼齿有第二后附尖。这一近裔性状，在犬族中只有狼类才有。

词源 希腊语，*Eu*：原始的；*cyon*：犬。

归入种 除 *Canis davisi* 及其同物异名（*Vulpes shermanensis* Hibbard，1937 和 *Canis condoni* Shotwell，1956）外，还有“*Canis*” *monticinensis* Rook，1992，*Canis chiliensis minor* Teilhard de Chardin，1930，*Eucyon zhoui* n. sp. 此外显然还有 *Vulpes odessana* Odintzov，1967。

分布 最早出现于北美晚中中新世克拉任冬期（Clarendonian，一新种待发表）；属型种发现于整个晚中新世地层中，但以晚海费里期的化石最多。在欧亚大陆发现的有意大利最晚中新世，即晚土洛里期（Turolian）的 *E. monticinensis*，中国榆社上新世的 *E. davisi* 和 *E. zhoui*，泥河湾期的 *E. minor*，以及乌克兰露西尼期（Ruscinian）的 *E. odessana*。

Eucyon davisi (Merriam), 1911

? *Canis* sp. Zdansky, 1927

材料 云簇次盆地：刘家沟：美国自然历史博物馆标本编号 F: AM 97031，右下颌带犬齿和全部颊齿；泥河次盆地：峡口附近：F: AM 97027，几近完整的头骨和齿列；F: AM 97028，破碎头骨和部分齿列；F: AM 97056，完整头骨带齿列（图 1）；F: AM 97057，几近完整的头骨和齿列；F: AM 97058，破碎头骨及下颌，带近乎完整的齿列（图 1）；F: AM 97059，残破头骨前半部，齿列几近完整；F: AM 97061，上腭带完整齿列。泥河村附近（桑志华第 25 地点）：中科院古脊椎所标本编号 V12182（桑志华标本原编号THP 22818），部分头骨和齿列；泥河掌附近（张八沟，Zdansky，1927），左下颌带犬齿和前臼齿。

讨论 在牙齿和头骨的大小上，峡口标本和北美晚海费里期的居群相合。和欧洲晚中新世的*E. monticinensis* 相比，正如Rook 1992 年所指出的，它的下颌水平支更高，下裂齿的下内尖与下次尖相比较小，下原尖（和三角座）更窄，上第一臼齿通常有前附尖，而且挠—胫骨的比例象狐者一样，小于 80%. 这个种和新种 *E. zhoui* 的不同将在后者的特征中述及。它和 *E. minor* 的区别是它的下第二臼齿的跟座更长，所以整个牙齿相对于下裂齿而言就更长些，而且其下颌水平支也较低。*E. davisi* 在中国上新世地层的出现使其地史和地理的分布更广了。这样它就和另一些北美的种类，例如驼类（*Paracamelus* 属在北美是否存在至今还没有完全肯定），短吻嵌齿象 *Sinomastodon*（它和 *Stegomastodon* 是否能分开还有疑问），兔类中的 *Hypolagus*，犬类中的 *Vulpes*，*Nyctereutes*，和 *Canis*（见Flynn *et al.*，1991）共生。它们都是上新世时迁徙至亚洲的。在北美，*E. davisi* 虽然在最晚中新世时和 *Canis* 及 *Vulpes* 共生，在上新世却无记录。这样，这个种延续的时间就特别长，从大约 9 Ma 直到 2.5 Ma，亦即生存了 6.5 个

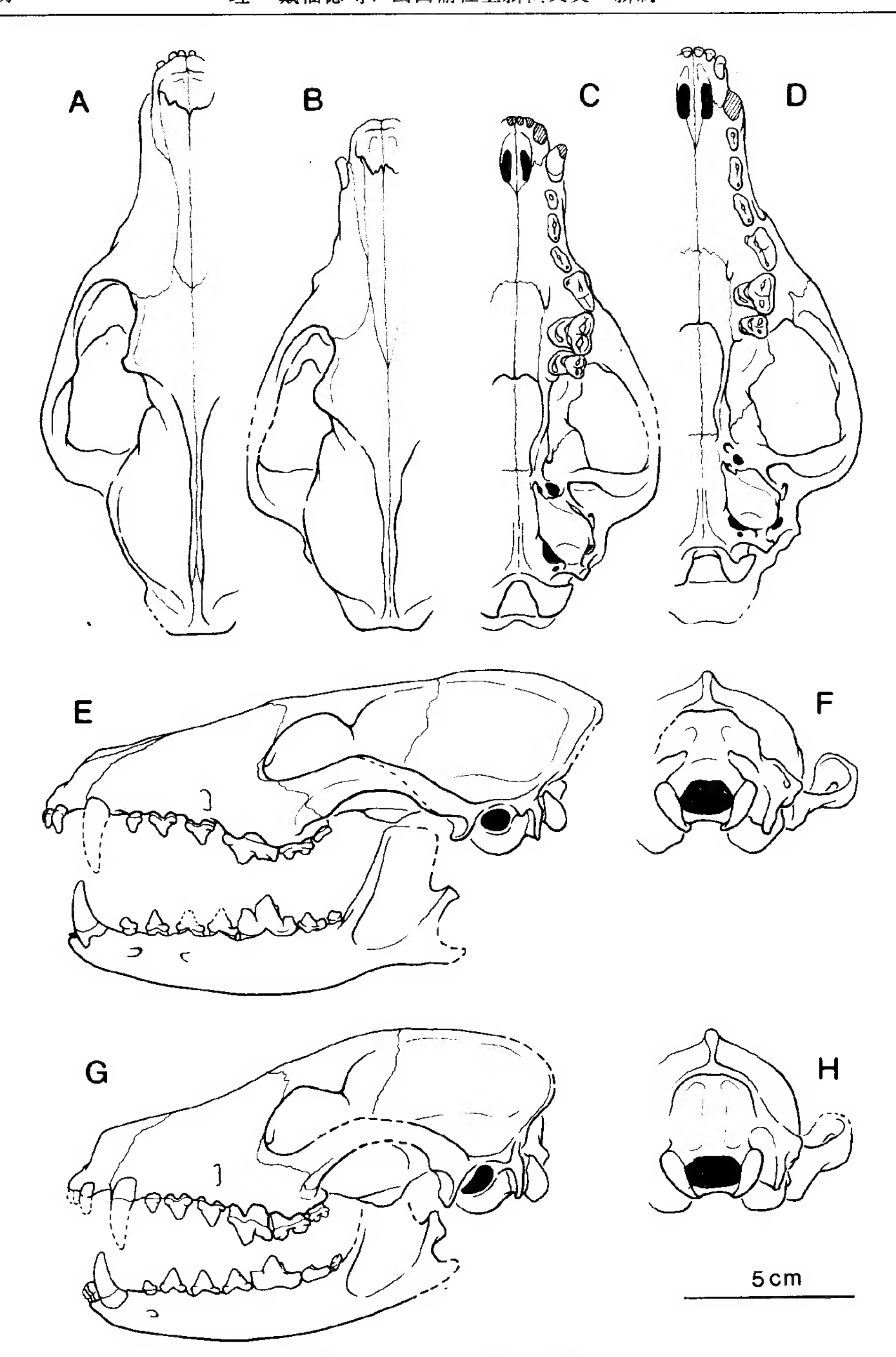


图 1　*Eucyon* 两个种的比较

E. davisi: 头骨: F: AM 97056, B,C,G,H; 下颌: F: AM 97058, G;

E. zhoui: 正型: V12181 (THP 10199), A,D,E,F

Fig.1　Comparative views of *Eucyon davisi*, referred skull, F: AM 97056, B,C,G,H, and mandible, F: AM 97058, G; and *E. zhoui*, holotype, V12181 (THP 10199), A,D,E,F

百万年。Rook 的文章表明，这个属在意大利（Brisighella）和西班牙（Venta del Moro，MN13）都出现于最晚中新世。在欧洲这看来是最早的出现。它和在北美该种最晚的出现显然是同时的。感谢莫斯科地质研究所 M. Sotnikova 的友善，本文前一作者有幸观察了奥德萨上新世正型地点裂隙堆积中的 *Vulpes odessana* 的化石。测量结果表明，在大小和比例关系上，中国的 *E. davisi* 和 *V. odessana* 非常接近。牙齿和头骨的形态对比也证实了 *odessana* 确为 *Eucyon* 属的一个成员，它具有该属上述的关键特征。它和与它同时的中国的材料会不会是同一个种，这种可能性也是应该认真考虑的。不管怎样，这些材料表明，有一些和 *E. davisi* 很接近的种，在上新世时其地理分布已经扩散到了东欧。

Eucyon zhoui n. sp.

正型 V12181(THP 10199)：几乎完整的头骨和下颌，带完整齿列（图 2），采自泥河次盆地，银郊村。头骨因腹背向受压而稍变扁，矢状嵴后移超过枕大孔。

归入标本 云簇次盆地：V12183(THP 22928)：头骨的前、后部，带不完整齿列，采自赵庄麻则沟组下部或高庄组上部；榆社县博物馆未编号标本：几乎完整的头骨，腹背向受压，只有第一、二、四前臼齿和臼齿，采自高庄村高庄组上部，可能是醋柳沟段；天津自然博物馆未编号标本：几乎完整头骨和部分下颌，侧向压扁，齿列完整，采自高庄附近；F：AM 97048，头骨前部，带下颌，几乎完整的齿列，采自赵庄附近，麻则沟组下部或高庄组上部。

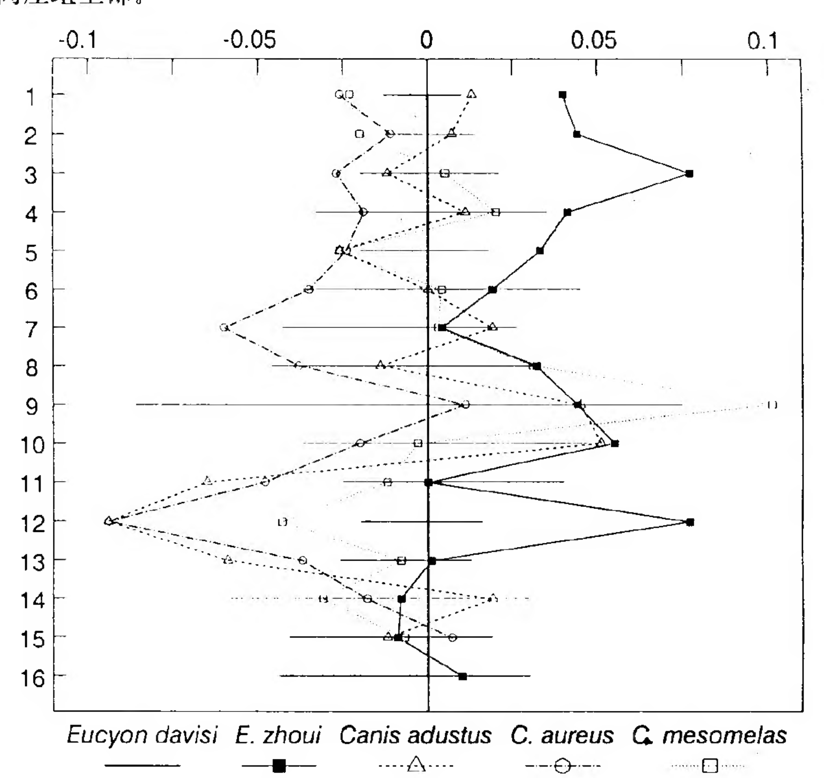


图2 *Eucyon davisi*和*E. zhoui*及非洲豺的头骨对数比率图 (Simpson 1941)

E. davisi(对比基), 峡口材料, 七个个体, 横线代表观测范围;

E. zhoui, 材料见该种描述部分, 五个个体, 仅取均数;

非洲豺, 美国自然历史博物馆哺乳动物部材料, 共28个个体。

测量: 1. 犬齿齿槽后缘至枕大孔凹之间的距离; 2. 头骨最大长: 前颌骨前缘至枕顶后端; 3. 头骨颧弓处最大宽; 4. 脑颅部最大宽; 5. 上齿列长; 6. 上齿列外缘最大宽; 7. 上腭在P1齿槽内缘处之宽; 8. 头骨眶后突处最大宽; 9. 眶后收缩处之最小宽; 10. M2后缘至听泡前缘之间的距离; 11. 齿槽至眶下缘之间的距离; 12. 颧骨在眶后突之前的最小垂直高度; 13. P4外缘最大长; 14. M2最大宽; 15. 听泡长; 16. 听泡最大宽

Fig.2 Log-ratio diagram (Simpson, 1941) comparing the cranial proportions of *Eucyon zhoui* and three sympatric African jackals with *Eucyon davisi* (standard of comparison) using the following measures: 1. Length: distance from posterior border of canine alveolus to foramen magnum notch; 2. Greatest length: Anterior tip of premaxillae to posterior point of inion; 3. Zygomatic width: greatest distance across zygomata; 4. Braincase width: Maximum breadth of braincase across level of parieto-temporal sutures; 5. Maxillary tooth row length: anterior edge of alveolus of P^1 to posterior edge of alveolus M^2; 6. Maximum width across upper cheek teeth: between outer sides of most widely separated teeth (P^4 or M^1); 7. Palatal width at P^1: Minimum width between inner margins of alveoli; 8. Frontal shield width: Maximum breadth across post-orbital processes; 9. Post-orbital constriction: least width across frontals at constriction behind post-orbital processes; 10. Length M^2 to bulla: minimum distance from posterior edge of alveolus of M^2 to depression in front of bulla; 11. Height, maxillary tooth jaw to orbit: Minimum distance from outer alveolar margin of M^1 to most ventral point of orbit; 12. Jugal depth: Minimum depth of jugal anterior to postorbital process, at right angle to its anteroposterior axis; 13. P^4 length: Maximum anteroposterior length measured on outer side; 14. M^2 width: Maximum transverse diameter; 15. Bulla length: from median lacerate foramen to suture of bulla with paroccipital process; 16. Bulla width: maximum width from suture with mastoid process to medial side. *Eucyon davisi* represented by the Xiagou sample (N=7), observed range (horizontal bars) and mean shown. *Eucyon zhoui* represented by hypodigm (N=5) listed herein, mean only plotted. The three sympatric jackals from Kenya are contained in the Department of Mammalogy, American Museum of Natural History collections: *Canis adustus bweha* (N=6, samples of adult males, N=3; females N=3), *Canis aureus bea* (N=6, samples of adult males, N=2; females N=4), and *Canis mesomelas elgonae* (N=6, samples of adult males, N=3, females N=3)

分布 高庄组上部, 也可能麻则沟组下部, 云簇次盆地和泥河次盆地的相应地层。晚吉伯特至早高斯磁性年代地层期。

特征 头骨比*E. davisi*的大。区别主要表现在下列特征 (见括号内编号) 和头长的比例关系上 (图2): 上腭在第一前臼齿处的宽度 (7) 较窄, 但头骨在颧弓处 (3) 则

较宽，颞窝(10)长，上颌骨在眶下的高度(11)小，颧骨(12)深，第四前臼齿(13)短，第二臼齿(14)窄，耳泡(15)小，但较宽(16)，球形悬垂；乳突为一腹背向嵴；鼻骨向后不超过上颌骨—额骨骨缝，其后端宽，不呈尖角状；第一臼齿的前尖大于后尖；中翼肌上支在角突上的附着面和 *Canis* 属的一样大。

词源 以古脊椎动物与古人类研究所前所长和北京自然博物馆馆长，建国以来对中国古脊椎动物学作出重要贡献的周明镇教授命名。

讨论 正如在特征中所指出的，它和榆社的 *E. davisi* 标本的区别主要是在头骨的大小和比例上（图3）。虽然新种的牙齿在绝对大小上总是比 *E. davisi* 偏大，但还是有相当部分的重叠，而且与整个头骨相比还是较小。类似的差别在坦桑尼亚的三种现生豺中也可以见到。目前还不能完全肯定上述两个种是否真在云簇次盆地中共生，因为发现的材料还很少。就现有的材料看，似乎 *E. zhoui* 出现得较早些。

在法国的 St. Esteve(MN15) 的中上新世地层中 Martin(1973) 记述了一个和 *E. zhoui* 大小相近而又同时代的种，*Canis adoxus*。Rook (1992) 把它和 *E. monticinensis*

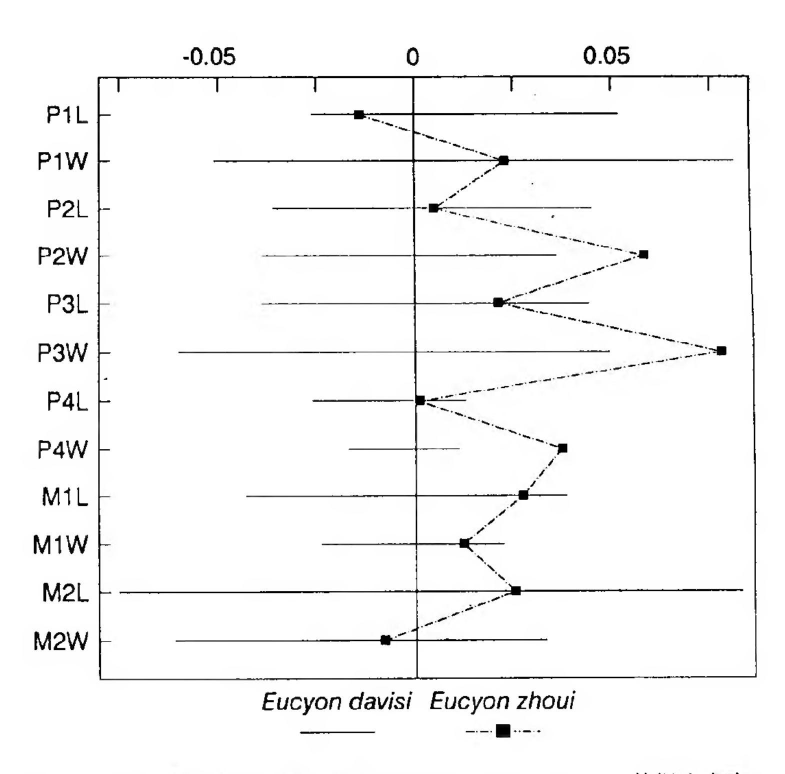


图3 *Eucyon* 两个种的牙齿对数比率图 (Simpson 1941)，数据取自表1
E. davisi (对比基)，峡口材料，七个个体，横线为观测数据；
E. zhoui，五个个体，仅取均数

Fig.3 Log-ratio diagram (Simpson, 1941) of measurements of the upper dentition, comparing the size and relative proportions of *E. davisi* (the Xiakou sample, N=7) as the standard, observed range shown, with the mean of the hypodigm (N=5) of *E. zhoui*. Data from Table 1

区别开来，因为前者大，吻部长而前臼齿退化。*Canis adoxus* 和榆社的 *E. davisi* 也有这些区别。但是它比两个中国的种都更进步：它的第三上门齿更大，额窦扩展至眶后突上，枕面亚三角形（后视），其顶端悬垂在枕髁之上（侧视），臼齿的前附尖都小，下颌的角突短而深，其中翼肌下支的附着面较大。Pons-Moya 和Crusafont-Pairo早就指出过(1976)，“*Canis*” *adoxus* 显然不能归入狐类。但是它的某些进步特征和犬亚科为共近裔性状。这使我们相信，“*C.*” *adoxus* 也不能归入 *Eucyon* 属。

Eucyon zhoui 有三点与犬族为共近裔性状：上臼齿的前尖大于后尖；中翼肌上支附着区大和第四下前臼齿具第二后附尖。将来如有更多的证据，也可能表明它和犬族确有更近的系统关系。

表 1　*Eucyon* 两个种头骨和牙齿的测量 [1)]　　(单位：毫米)

Table 1　Measurements of the skulls and teeth of *Eucyon davisi* and *E. zhoui*　　(in mm)

		Eucyon davisi							*Eucyon zhoui*				
Measurements		F:AM 97027	F:AM 97028	F:AM 97059	F:AM 97061	F:AM 97056	F:AM 97057	F:AM 97058	THP uncat.	THP 22928	YM uncat.	F:AM 97048	V 12181
cranial	1	118.5				123.0	125.0				134.7		133.1
	2	152.1				156.0	162.0		170.5		172.8		177.4
	3		86.0	81.0		88.0		80.0					100.0
	4	46.7				54.4	53.3	46.5		51.7	54.0		60.0
	5	53.5	58.5	56.7	55.9	56.0	54.3	57.6	62.2	58.5	59.1	61.9	60.8
	6	48.0		44.3	47.0	53.5	48.9	48.0			47.8	52.0	51.5
	7			16.7	18.7	19.6	18.8	18.4	16.6	16.0	17.4	21.0	20.0
	8	40.0				40.8	43.2	36.0	38.5	41.0	48.0		44.6
	9	21.6				30.0	31.3	22.5	26.0		33.4		28.1
	10	34.5	36.0			38.5	41.8	36.9	37.7		47.5		42.5
	11	20.6	22.3	19.5		20.0	20.3	19.2	20.8	22.0	17.5	21.0	20.4
	12		10.0	9.7				9.2	11.0				12.0
	13	14.8	16.0	16.2	16.1	15.4	15.6	16.0	15.6	15.0	15.0	16.9	16.3
	14	7.9	8.7	8.2	9.6	9.8	9.6	9.8	7.8	8.2	9.8	9.9	8.9
	15	22.5	20.0			22.0	23.0	22.5	20.5	21.7	21.4		22.6
	16	16.4	14.5			17.2	16.2	16.0	15.3	14.8	17.4		18.3
upper teeth	P1L		6.1	5.2	5.1	5.2	5.1	5.8	5.3	5.9	4.2	5.3	5.5
	P1W		3.2	3.1	3.0	2.8	3.0	3.8	3.2	3.5	2.7	3.5	3.7
	P2L	8.6	10.0	9.1	9.2	8.3		8.9		9.2	7.8	10.0	9.5
	P2W	3.4	3.2	3.7	3.4	3.5		3.8		4.2	3.7	4.1	4.0
	P3L	9.8	11.5	10.8	10.5	9.5		10.2	10.6		10.0	11.8	11.2
	P3W	4.5	3.5	4.2	3.8	4.0		4.1	4.6			4.9	4.9
	P4L	14.8	16.0	16.2	16.1	15.4	15.6	16.0	15.6	15.0	15.0	16.9	16.3
	P4W	8.2	7.8	8.1	8.0	8.0	7.7	8.2	8.5	9.0	7.8	8.7	9.6
	M1L	9.9	11.2	9.8	11.0	11.8	10.8	11.2	10.4	11.2	12.6	11.0	12.1
	M1W	12.5	13.4	13.0	12.8	13.5	13.9	13.4	12.6	12.9	13.9	14.0	14.6
	M2L	5.5	5.5	6.2	7.0	7.6	7.9	6.1	6.4		7.2	7.0	7.1
	M2W	7.9	8.7	8.2	9.6	9.8	9.6	9.8	7.8	8.2	9.8	9.9	8.9
lower teeth	p1L							5.2	4.1			4.4	4.8
	p1W							3.1	3.2			3.1	3.2
	p2L							8.8	8.8			9.3	8.6
	p2W							3.7	4.0			4.1	3.8
	p3L							9.7	9.8			10.6	
	p3W							3.8	4.0			4.5	
	p4L							10.9	11.4			11.2	11.7
	p4W							4.9	5.2			5.5	5.5
	m1L							17.8	17.1			17.9	18.2
	m1WTr							6.6	7.0			6.6	7.8
	m1WTl							6.6	6.4			6.6	8.1
	m2L							7.8	8.3			7.8	9.0
	m2W							5.8	6.2			5.8	7.0
	m3L							4.3	3.5			4.3	5.6
	m3W							3.6	3.3			3.6	3.8

1) Numbered skull dimensions follows that detailed in the legend of Fig. 2; measurements of teeth follow standard procedures for length (L) or width (W)

结 论

新属 *Eucyon* 系为新、旧大陆犬亚科中一些位于系统发育基部的种所建。在北美它最早出现于中中新世，早于 *Canis* 和南美犬类的出现（都是晚中新世）。*E. davisi* 在早上新世时从美洲迁徙入东亚，同时出现的还有 *E. zhoui*。在新大陆没有发现与其相对应的种。这表明，这个属在晚中新世的分异发生在它在亚洲出现之前。这些原始的犬类在榆社盆地延续至晚上新世，那时如狼大小的 *Canis* 已首次出现。

参 考 文 献

Berta A, 1988. Quarternary evolution and biogeography of the large South American Canidae (Mammalia: Carnivora). *Univ. Calif. Publ., Geol. Sci.*, **132**: 1—149.

Flynn L J, Tedford R H, Qiu Z X, 1991. Environment and stability in the Pliocene Mammalian fauna of North China. *Paleobiology*, **17**: 246—265.

Martin R, 1973. Trois nouvelles espèces de Caninae (Canidae, Carnivora) des gisements Plio-Villafranchiens d'Europe. *Docum. Lab. Géol. Fac. Sci. Lyons*, **57**: 87—96.

Merriam J C, 1911. Tertiary mammal beds of Virgin Valley and Thousand Creek in northwestern Nevada, Part II—— Vertebrate Fauna. *Univ. Calif. Publ., Bull. Dept. Geol.*, **6**: 199—304.

Odintzov I A, 1967. New species of Pliocene Carnivora, *Vulpes odessana* sp. nov., from the Karst Cave of Odessa. *Paleontologichesky Sbornik* (*Lwov University*), **4**: 130—137.

Opdyke N, Mein P, Moissenet E *et al.*, 1989. The magnetic stratigraphy of the late Miocene sediments of the Cabriel Basin, Spain. In: Lindsay E H *et al.* eds. European Neogene Mammal Chronology. New York: Plenum Press, 1990, 507—525.

Pons-Moya J, Crusafont-Pairo M, 1979. Sobre la identidad del "*Canis*" *adoxus* Martin (1973) y su implicación en el conocimiento de género *Vulpes*. *Acta Geol. Hispanica*, **2** (1978): 129—132.

Rook L, 1992. "*Canis*" *monticiensis* sp. nov., a new Canidae (Carnivora, Mammalia) from the late Messinian of Italy. *Boll. Soc. Paleon. Italiana*, **31**: 151—156.

Simpson G G, 1941. Large Pleistocene felines of North America. *Am. Mus. Novit.*, (1136): 27pp.

Tedford R H, Taylor, B E (MS). North American fossil Canidae (Mammalia: Carnivora): The Caninae.

Zdansky O, 1927. Weitere Bemerkungen über fossile Carnivoren aus China. *Palaeont. Sinica*, Sec. C., **4** (4): 1—28.

A NEW CANID GENUS FROM THE PLIOCENE OF YUSHE, SHANXI PROVINCE

Richard H. Tedford
(*American Museum of Natural History* New York 10024)

Qiu Zhanxiang
(*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences* Beijing 100044)

Key words Yushe, Shanxi, Pliocene, Canidae

During the course of review of the phylogeny of the fossil North American taxa of the canid subfamily Caninae, Tedford and Taylor (MS) were able to recognize that the taxon *Canis davisi* Merriam, 1911, from the early Hemphillian of Oregon, and defined on a maxillary fragment bearing M^{1-2}, could be associated with abundant material representing all elements of the skeleton from correlative and later Hemphillian (late Miocene) deposits of the United States. Study of these materials in the course of a cladistic analysis of phylogeny revealed that *C. davisi* assumed the position of a stem-taxon for both the South American genera and the *Canis*-group of derived forms. This view was published by Berta (1988) in her analysis of the larger South American canids which include representatives of both of the indicated clades.

It now appears that this stem group is represented by a number of species present at Pliocene localities scattered across Eurasia. Current research on these samples necessitates the description of the taxon in advance of the monographic work that first brought it to light. The sample from the Gaozhuang and Mazegou formations from the Yuncu Subbasin, and correlative rocks in the Nihe Subbasin, Yushe Basin, includes uncrushed or little deformed crania and associated rami that more satisfactorily depict the cranial features diagnostic of the new genus and so introduction of it by these specimens seems appropriate and an expedient way to transmit information to others now working with this taxon.

We recognize in taking this step that the new genus creates a paraphyletic taxon due to its relatively primitive position at the base of the Tribe Canini. We have not been able to recognize any of the species of the new genus as members of more derived clades, although the derived species, *Eucyon zhoui* n. sp., possesses some characters in common with the *Canis*-group and when better known might be regarded as a prmitive member of that clade.

Family Canidae Gray, 1821
Subfamily Caninae (Gray), 1821
Tribe Canini (Gray), 1821
Eucyon n. gen.

Genotypic species *E. davisi* (Merriam), 1911.

Diagnosis The new genus is distinguished from the fossil (*Leptocyon*) and living Vulpini (*Vulpes* s. l., *Urocyon* and *Otocyon*) by possession of three synapomorphies also possessed by all other members of the Canini (South American canines and *Canis*, *Cuon*, and *Lycaon*): A frontal sinus is present; it invades the base of the post-orbital process usually removing the "vulpine-crease" or depression on the dorsal surface of the process; the paroccipital process is expanded posteriorly and usually has a salient tip and the mastoid process is enlarged into a knob or ridge-like prominence. The Chinese material shows that *Eucyon*, like other Canini, has lost the fox–like lateral flare and eversion of the dorsal border of the orbital part of the zygoma. *Eucyon* lacks a feature characteristic of all other Canini, namely development of a transverse cristid connecting the hypoconid and entoconid of the M_1 talonid. On the other hand *Eucyon* species have, as an autapomorphy, a second posterior cusplet on the P_4 possessed only by the wolf group among the Canini.

Etymology Greek: *Eu*, primitive; *cyon*, dog.

Included species In addition to the genotypic species, *Canis davisi*, and its junior synonyms (*Vulpes shermanensis* Hibbard, 1937; and *Canis condoni* Shotwell, 1956), the genus also includes "*Canis*" *monticinensis* Rook, 1992, *Canis chiliensis minor* Teilhard and Piveteau, 1930, *Eucyon zhoui* n. sp. and apparently *Vulpes odessana* Odintzov, 1967.

Distribution The earliest occurrence of species of this genus are in the Clarendonian (late medial Miocene) of North America (a new species to be described elsewhere); the genotypic species, *E. davisi*, occurs throughout the North American Hemphillian (late Miocene) although the late Hemphillian populations are the best known. In Eurasia species of the genus are known from the latest Miocene, late Turolian (*E. monticinensis*) of Italy, and Pliocene, Yushean (*E. davisi*, *E. zhoui* n. sp.) and Nihewanian (*E. minor*) of China, Ruscinian (*E. odessana*) of Ukraine.

Eucyon davisi (Merriam), 1911

? *Canis* sp. Zdansky, 1927

Material From the Yuncu Subbasin. Liujiagou: F: AM 97031, right ramus

with canine, P_1-M_3. From the Nihe Subbasin. Near Xiakou: F: AM 97027 nearly complete skull and dentition; F: AM 97028, crushed skull and partial dentition; F: AM 97056 complete skull and dentition (Fig 1); F: AM 97057, nearly complete skull and dentition; F: AM 97058, broken skull and associated mandible (Fig. 1) with nearly complete dentition; F: AM 97059, anterior part of skull, crushed, nearly complete dentition; F: AM 97061 palate with complete dentition. Near Nihecun (Licent Locality 25): V12182 (THP 22818), partial skull with partial dentition. Near Nihezhang (Chang Pa Kou, Zdansky, 1927, pp. 5-6, plate 1, fig. 1-2), left ramus with canine, P_{1-4}. Measurements of Xiakou sample, Table 1.

Occurrence In the Yushe Basin this taxon is principally represented in the Nihe Subbasin from poorly localized sites near Xiakou, Nihecun and Nihezhang. The Frick Collection contains a suite of fossils from near Xiakou, including the *Eucyon* material, all of which shows the same preservation and adhearing matrix. The taxa accompanying *E. davisi* include *Proboscidipparion pater*, *Cremohipparion licenti*, *Gazella* cf. *blacki* and *Pliohyaena* sp. that indicate a late Yushean age. A similar fauna occurs in the younger strata cropping out around Nihezhang and Nihecun. The ramus from Liujiagou, in the Yuncu Subbasin, occurs in the upper part of the Mazegou Formation associated with a fauna of late Yushean age in strata belonging to the later part of the Gauss Chron.

Discussion In dental dimensions, and those of the skull (as far as these can be determined from the North American record), the Xikgou sample agrees with *E. davisi* populations from late Hemphillian sites in North America. It differs from the European late Miocene *E. monticinensis*, as Rook (1992) has pointed out, in having a deeper horizontal ramus of the mandible, the entoconid of M_1 is smaller relative to the hypoconid and the protoconid (and trigonid) is more slender, the M^1 parastyle is usually present and the radius/tibia ratio is less than 80% as in vulpines. *Eucyon davisi* differs from *E. zhoui* n. sp. as indicated in the diagnosis of the latter and it differs from *E. minor* in having a longer M_2 talonid resulting in a less reduced M_2 relative to M_1, and a shallower horizontal ramus.

The presence of *Eucyon davisi* in Pliocene rocks in China extends the geographic and geologic range of this taxon. It thus accompanied such other North American taxa as the Camelidae (e. g., *Paracamelus*, a genus not so far positively identified in North America), the brevirostrine gomphotheriid *Sinomastodon* (doubtfully separable from *Stegomastodon*), the leporid *Hypolagus*, and the canines *Vulpes*, *Nyctereutes*, and *Canis* (Flynn *et al.*, 1991) as Pliocene immigrants to Asia. There is no Pliocene record of *E. davisi* in North America although the taxon coexisted with both *Canis* and *Vulpes* in the latest Miocene. Its

extension into the Pliocene, perhaps as young as 2.5 Ma, gives this taxon an enormous temporal range from about 9 Ma to 2.5 Ma or a 6.5 million year biochron. Rook's work (1992) has shown that the genus *Eucyon*, and a species closely related to *E. davisi*, *E. monticinensis*, occurs in late Turolian (latest Miocene) strata in Italy (Brisighella) and Spain (Venta del Moro, MN13, Chron 5, Opdyke *et al.*, 1989). This appears to be the oldest known occurrence of the genus in Eurasia and clearly contemporaneous with the latest occurrence of *E. davisi* in North America.

Through the kindness of M. Sotnikova of the Geological Institute, Moscow, the senior author was able to examine a sample of *Vulpes odessana* Odentzov, 1967, from the early Pliocene (Ruscinian) fissure fills of Odessa, the type locality. Measurements established the close size and proportional relationships of the cranium and dentition between *V. odessana* and the Chinese *E. davisi* sample. Morphological comparison of the dentition and cranial roof confirmed the presence of the key features listed above in the diagnosis of *Eucyon* indicating that *odessana* is a member of that genus. The possibility that the coevel Chinese and Ukrainian forms belong to the same taxon must be seriously considered. In any event the material shows that forms closely allied to *E. davisi* had a geographic range extending to eastern Europe in the Pliocene.

***Eucyon zhoui* n. sp.**

Holotype V12181 (THP 10199), nearly complete skull and mandible with complete dentition (Fig 1); from near Yinjiao village; Nihe Subbasin. Dorso-ventral crushing has slightly flattened the skull and pushed the lambdoidal .crest back over the foramen magnum.

Referred specimens Yuncu Subbasin: V12183 (THP 22928), anterior and posterior parts of skull with incomplete dentition, from Zhaozhuang Village, lower Mazegou or upper Gaozhuang formations, Yuncu Subbasin; Yushe Museum, uncatalogued, nearly complete skull dorso-ventrally crushed, lacking all tooth crowns except P^{1-2}, P^4 and M^{1-2}, Gaozhuang village, upper Gaozhuang Formation, probably Nanzhuanggou Member; THP uncatalogued, nearly complete skull and partial mandible, medio-laterally crushed, nearly complete dentition also from the vicinity of Gaozhuang Village; F: AM 97048, anterior part of skull and associated mandible with nearly complete dentition; near Zhaozhuang Village, lower Mazegou or upper Gaozhuang formations. Measurements of hypodigm, Table 1.

Distribution Upper Gaozhuang and possibly lower Mazegou formations, Yuncu subbasin, presumably equivalent stratigraphic position in the Nihe

Subbasin. Late Gilbert to early Gauss chrons.

Diagnosis Skull larger than *Eucyon davisi*. Distinguished by the following proportional relationships relative to skull length (Fig. 2, numbered features in parentheses): palate narrower across P^1 (7), but skull is wider across zygoma (3); longer temporal fossa (10); shallower maxillary beneath orbit (11); deeper jugal (12); shorter P^4 (13); narrower M^2 (14); and bulla small (15), wider for length (16), globular and pendant; mastoid process a dorso-ventral ridge; nasals do not extend behind maxillary-frontal suture, and they are broad rather than pointed at their termination; M^1 paracone larger than metacone; insertion of superior ramus of median pterygoid muscle on angular process enlarged as in *Canis*.

Etymology Named for Prof. Zhou Minzhen, Emeritus Director of IVPP and Beijing Natural History Museum and a leader in Chinese vertebrate paleontology since 1949.

Discussion As indicated in the diagnosis, the principle distinctions between *E. zhoui* and the Yushe sample of *E. davisi* are proportional features of the skull (Fig. 2). There is considerable overlap in dental dimensions although the small samples show a persistently larger absolute size of the teeth of *E. zhoui* (Fig. 3), but a smaller size relative to the skull as a whole. These types of proportional differences (Fig. 2) characterize the skulls of the three sympatric living jackal species in Tanzania (*C. adustus*, *C. mesomelas* and *C. aureus*). It cannot be clearly demonstrated that *E. davisi* and *E. zhoui* were coexistent because of the rarity of the former in the Yuncu Subbasin and vice-versa. The available record indicates that *Eucyon zhoui* occurs in older strata of late Gilbert and early Gauss age.

In medial Pliocene deposits at St. Estéve, France, correlated with the Ruscinian fauna of Perpignan (MN15) of early Gauss age, Martin (1973) described *Canis adoxus*, a form similar in size, and contemporaneous with *E. zhoui*. Rook (1992) has differentiated "*C.*" *adoxus* from *E. monticinensis* by the former's larger size, elongate nuzzle and reduced premolars. It differs from Yushe *E. davisi* in the same way. It is more derived than either of the Chinese taxa in the relative enlargement of I^3, expansion of the frontal sinus into the postorbital process, the subtriangular shape at the occiput (viewed from the rear) whose inion overhangs the condyles (in lateral view), the small M^{1-2} parastyles, and an angular process of the mandible that is short and deep with an expanded fossa for the inferior ramus of the medial pterygoid muscle. Although "*C.*" *adoxus* is clearly not a vulpine as claimed by Pons Moya and Crusafont (1976), some of the derived features it displays are synapomorphies for other canine lineages. On this basis we believe "*C.*" *adoxus* should not be assigned to *Eucyon*.

Eucyon zhoui has three features that are synapomorphous with the *Canis*-group:

enlargement of paracone over metacone on the upper molars; enlargement of the area of insertion of the superior branch of the median pterygoid; and presence of a second posterior cusplet on P_4 (a character shared with *E. davisi*). Otherwise this taxon remains a primitive member of the Canini and these advanced features are considered autapomorphies of *E. zhoui*. It is possible that further evidence may strengthen a phyletic relationship with the *Canis*-group.

Conclusions

The new genus *Eucyon* is proposed for a group of species of Caninae that phylogenetically lie at the base of the derived clades representing the differentiation of the canines in the New and Old World. In agreement with its phylogenetic position, species of *Eucyon* appear in mid-Miocene deposits in North America predating the appearance of *Canis* (late Miocene) or members of the South American clade (late Miocene). *Eucyon davisi* appears in China in the early Pliocene as an immigrant from America, along with *E. zhoui* n. sp. that has no New World counterpart, suggesting later Miocene differentiation in the genus prior to its appearance in the Asian record. These primitive canids continue into the late Pliocene where they are joined by the earliest appearance of wolf-sized *Canis* in the Yushe Basin.